

STUDIES IN THE XYLARIACEAE: I. NEW AND OLD CONCEPTS*

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INTRODUCTION

The Xylariaceae have long been regarded as one of the most specialized groups of the Ascomycetes. Their large size, great variety of form and colour, and a relatively high level of differentiation are matched by few other families, and indeed make them unique among the Fungi.

Winter (1887) established the family to include all the Pyrenomycetes with predominantly dark stromata and dark unicelled spores, a concept subsequently embodied in important work by Miller (1928*a*, 1928*b*) and Dennis (1956, 1957). A different idea of the family was put forward by von Arx and Müller (1954, pp. 135 and 276) when they distinguished it on microscopical features alone, comprising club-shaped or cylindrical unituminate asci, each containing a complex apical structure, and dark unicelled spores with germ pores or germ slits. In the writer's view this is too drastic a revision because of the inclusion of many non-stromatic genera which possess various complexities of their own and do not figure in the anatomic specialization of the stromatic members. The writer, however, accepts that the detailed characters of von Arx and Müller in conjunction with the stromal features outlined by the earlier authors do provide a reasonable basis for definition of the Xylariaceae.

Identification of the various genera has been often fraught with a similar clash of opposing concepts. Recognition of an appropriate system of classification has been slow, mainly because the early workers of the nineteenth century gave undue emphasis to obvious but rather variable characters such as external form and colouration. Part of the problem consists of determining which are the most useful characters and which should most easily be discarded.

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The classical features employed in classification are:

- (1) Colour, size and shape of stroma;
- (2) Depth to which the stroma is sunken in the substrate, and whether superficial or erumpent;
- (3) Number and shape of perithecia;
- (4) Spore size and colouration; less frequently, spore shape.

The writer believes that these characters are useful in conjunction but not when taken singly. Furthermore, they have been used to the almost complete exclusion of several other characters which are as reliable if not more so. However, the latter require microscopic investigation and are often hard to determine. Another factor that is poorly understood is the relative importance that should be attached to each character. They may be divided into two categories:

- (1) Those which show a degree of correlation with a set of several other characters, and are present in a large number of the taxonomic variants. The value of these characters increases according to the completeness of the correlation and it is on these that genera are customarily founded because they usually express a single "idea" or theme. Much of the confusion in taxonomy is caused by the occurrence of two or more dominant features associated with overlapping sets of subordinates, on the relative value of which the investigator has to make a subjective judgement.
- (2) Those which are absolutely correlated with certain character groups and do not occur elsewhere, but whose frequency is not absolute. It is these which are hard to evaluate. When present in the majority of species of a taxon the writer is inclined to recognize it as of major importance; when only in a minority, however, its value is questionable.

No key to the currently accepted genera of the entire Xylariaceae has yet been written, but the following key, synthesized from the analytical work of von Arx & Müller (1954), Dennis (1957, p. 305), Hennings (1902, p. 16), Lloyd (1919), Miller (1928*b*, p. 336; 1942, p. 250; 1961, pp. 132-143) and Traverso (1906, pp. 21, 40, 57, 169, 173, 449, 475) is based on the criteria customarily used. Genera synonymous with these here, but discarded due to lesser priority, will be discussed in later papers.

A. Perithecia single or aggregated

I. Superficial

- a. Without protuberances
- aa. With conical protuberances

Rosellinia De Notaris (1844)
Stilbohypoxyton Hennings
 (1902)

II. Sunken in the substrate

- a. Valsoid
- aa. Dispersed or effuse

Anthostoma } *Lopadostoma* (Nitschke)
 Traverso (1906)
 Nitschke (1867) } *Anthostomella* Saccardo
 (1878, 1882)

- B. Perithecia several to many in the stroma
- I. Perithecia at the base of the stroma, with more or less elongated necks
- a. Perithecia polystichous *Bolinia* Nitschke (1867)
- aa. Perithecia monostichous
- i. Perithecia elongate
- j. Stroma aplanate *Camarops* Karsten (1873)
- jj. Stroma cylindric *Camillea* Fries (1849)
- ii. Perithecia ovate or oval
- j. Stroma effuse, perithecia very large *Theissenia* Maublanc (1914)
- jj. Stroma cupulate or effuso-convex *Nummularia* Tulasne (1863: Nomen invalidum) syn. *Numulariola* House (1925)
- jjj. Stroma effuse repand, with subcoriaceous peridium *Peridoxylon* Shear (1923)
- II. Perithecia seated at the periphery of the stroma, monostichous or occasionally polystichous
- a. Ostioles absent or obsolescent *Phylacia* Léveillé (1845)
- aa. Ostioles present
- i. Stroma variously shaped but not stipitate
- j. Stroma light coloured, inside gelatinous and hollow *Entonaema* Möller (1901) syn. *Sarcoxydon* Cooke (1883)
- jj. Stroma light, inside fleshy *Penzigia* Saccardo (1888, 1892)
- jjj. Stroma dark, inside corky
- k. Interior concolorous *Hypoxydon* Bulliard (1791)
- kk. Interior zonate *Daldinia* Cesati & De Notaris (1863)
- ii. Stroma broadly clavate to filiform or capitate, simple or branched, definitely stipitate
- j. Sterile portion of stroma formed of strands, fertile portion clavate *Thamnomycetes* Ehrenberg (1820)
- jj. Sterile portion of stroma not formed of strands
- k. Fertile stroma capitate, forming an expanded disc in which the perithecia are uniformly distributed
- l. Caespitose, on wood *Kretzschmaria* Fries (1849)
- ll. Not caespitose, on dung *Poronia* Gleditsch ex Wildenow (1787)
- kk. Fertile stroma clavate or filiform
- l. Occurring on wood *Xylaria* Hill ex Fr. (1751)
- ll. Occurring on dung *Podosordaria* Ellis & Holway (1897)

It is the object of this and succeeding papers to supplement this classification and to amend it where necessary, giving the most weight to those sets of features which show the maximum degree of intra-correlation and which also show the least variability.

MATERIALS AND METHODS

Herbarium and fresh material were investigated according to standard methods, and precise descriptions drawn up for each specimen. Damaged or very old material was rejected. Out of 1550 collected specimens the writer succeeded in culturing some 600 on 2% malt agar and then recording the gross characteristic of the colonies and those of the imperfect stage where formed.

The linear growth rate of colonies in plate culture at 25° was also determined according to the method of Brancato and Golding (1953). Whereas an adequate amount of material of the perfect stage was examined for each genus, it was unfortunately not possible to obtain as complete a representation of the cultural characters due either to the age of the specimen when collected in the field or to some innate peculiarity which prevented ready germination.

RESULTS

The following is an attempt to evaluate old and new characters as a result of this research.

A. Characters of the perfect stage.

1. *Geographic distribution.* The Xylariaceae are ubiquitous in distribution yet the family shows its greatest specialization of form in the tropics to which the genera *Kretzschmaria*, *Phylacia*, *Camillea* and *Thamnomycetes* are restricted. Although there have been abundant collections made of the tropical species, most of our knowledge of the family stems from the more intensive work done on the European and North American ones by mycologists resident in those countries. More information will probably reveal fairly clear cut differences in generic distribution which are at present too scanty to be used in classification. Many of the species may also be based primarily on differences in latitude of origin. For example, *Hypoxylon rubrostromaticum* Miller is the tropical counterpart of the northern *H. fuscum* Pers ex Fr. The two species show only minor differences in the perfect stages and could easily be confused, but the writer has found that *H. rubrostromaticum* grows faster and has a temperature tolerance of up to 33°C instead of 28°C, a factor which could have definite significance when further information is obtained on its tropical range.

Most of the Xylariaceae are inhabitants of wooded regions, but the range of the environment extends from mesic to semi-arid. *Xylaria fioriana* Sacc. has been found by the writer in South Africa in open scrub where the rainfall is less than 15 inches per annum. On the other hand the writer has also always found *Hypoxylon murcidum* B. and Br. in South Africa and in North America close to running water. Much more needs to be found out about the water requirements and physiology of these fungi before these can be incorporated in their taxonomy, and the problem is made more difficult in that it has been impossible up to now to rear stromata in culture.

2. *Substrate.* The vast majority of the species grows on dead wood but a significant few prefer nonlignaceous materials including earth, dung, dead leaves and fruit rind. This is interesting since it is correlated with lack of rigidity in the stroma and a lesser degree of differentiation (*Poronia*, *Podosordaria*). Otherwise, substrate differences have not been found important.

3. *Species host preference.* Species preference was found to be important in some cases but not above the specific level. The reason why some species are only found on certain trees is hard to determine. Some examples of this sort of specialization are:

SPECIES	HOST
<i>Hypoxylon sassafras</i>	<i>Umbellularia californica</i>
<i>Hypoxylon laurus</i>	<i>Sassafras</i> spp. and other Lauraceae
<i>Hypoxylon grandineum</i>	<i>Gleditschia triacanthos</i>
<i>Hypoxylon tinctor</i>	<i>Quercus</i> spp.
<i>Hypoxylon murcidum</i>	<i>Platanus occidentale</i>
<i>Xylaria fioriana</i>	<i>Olea capensis</i>
	<i>Aloe ferox</i>

4. *Shape of the stroma.* This is one of the most difficult of all the characters to evaluate. The shape may vary with the number of the perithecia per stroma—when uniperitheciate, the stroma will be globose or ovoid; when containing two or several perithecia, pulvinate or aplanopulvinate; and when multiperitheciate, usually aplanopulvinate, globose, or hemispheric. Thus the number of perithecia per stroma is a rather important character when it influences size. The writer, having seen the extent of variation within samples, is of the opinion that the *potential development* within a given range of variation is sometimes more important as a basis for making categories than the most commonly assumed state. Such factors are however bound to be subjectively treated in considering the limits of genera and species, for some some species appear to be characterized by uniperitheciate stromata and others by multiperitheciate, while in general the majority show both types. Even though only a relatively small number of specimens has been examined, however, it has been found difficult to support the traditional separation of *Rosellinia* from *Hypoxylon* based purely on perithecial number.

5. *Size relationships of the stroma.* The same remarks apply to these as to the stromal shape, since they are intimately related. The family contains two extremes, one where the stroma is much wider than high and another where height is dominant. Between them lie a group of intermediates with which other characters are also correlated. No longer is it satisfactory to call species with elongate stromata "*Xylaria*" and the aplanate ones "*Hypoxylon*"; the position of many species can only be estimated by the juggling of many other characters in addition.

6. *Branching of the stroma.* This character is restricted to *Thamnomycetes*, *Kretzschmaria*, *Xylaria*, *Poronia* and *Podosordaria*. It has been a source of confusion for two reasons: first, because there are so many species in which it is variable, and second, because the fertile clavulae which the branches bear are in most cases directly comparable to the clavata of related unbranched species, i.e., the effect of branching does not materially influence morphology.

Hence it is debatable whether a branched stroma often differs significantly from an unbranched one for taxonomic purposes. Should the complex branching to the second or an indefinite degree on which the genus *Kretzschmaria* is based be regarded as sufficient to separate it from *Xylaria*, where the stroma is unbranched or branched to the first degree? Clearly we have a problem similar to that of perithecial number, and there is no ready objective method of evaluation.

7. *Fertility of the stroma.* Many of the Xylariaceae exhibit sterility of part of the stroma in their particular trend of specialization. In the aplanate stromata of *Hypoxyton* various areas in between the perithecia may be sterile, while the cylindric ones of *Kretzschmaria* and *Xylaria* develop stipes or slender apices. These characters are chiefly valuable at specific level only, yet have been used to delimit sections in the genus *Xylaria* (Fries, 1851).

8. *Subiculum.* This has been neglected almost totally. It is found in *Rosellinia*, *Penzigia*, *Kretzschmaria* and *Xylaria*. Basically the subiculum consists of any extrastromal mycelium not incorporated into the fertile portion. It is bright or dark coloured, crustose or matted, and contains five distinct branching types:

- (1) loose: sparingly branched and infrequently anastomosed; (Plate I:1)
- (2) ropy: sparingly or frequently branched, infrequently anastomosed but with several contiguous hyphae lying parallel and forming long cords; (Plate I:2)
- (3) reticulate: frequently branched but loosely anastomosed to form a net-like system; (Plate I:3)
- (4) close: frequently branched and clearly anastomosed to form a pseudo-parenchymatous mass (Plate I:5 and 6)
- (5) tentacular: similar to (3) but with short prong-shaped branches usually projecting; (Plate I:4)

This type has only been found in nature in association with *H. cantareirensis*.

The subiculum is interesting because its association with stromata of low specialization (*Rosellinia*) and with high specialization (*Kretzschmaria*, *Penzigia*, *Xylaria*) may indicate a line of direct development between the two. The stromatic construction of these genera has several points in common, the chief being the carbonaceous outer layer and the light coloured soft tissue beneath the perithecia and the general absence of colouration prevalent in the other genera. The various types of subiculum are distributed equally and so cannot be used to differentiate any genus or species group as a whole, but they are clearly of supplementary value as specific characters.

9. *The differentiation of the stroma.* This subject has been poorly under-

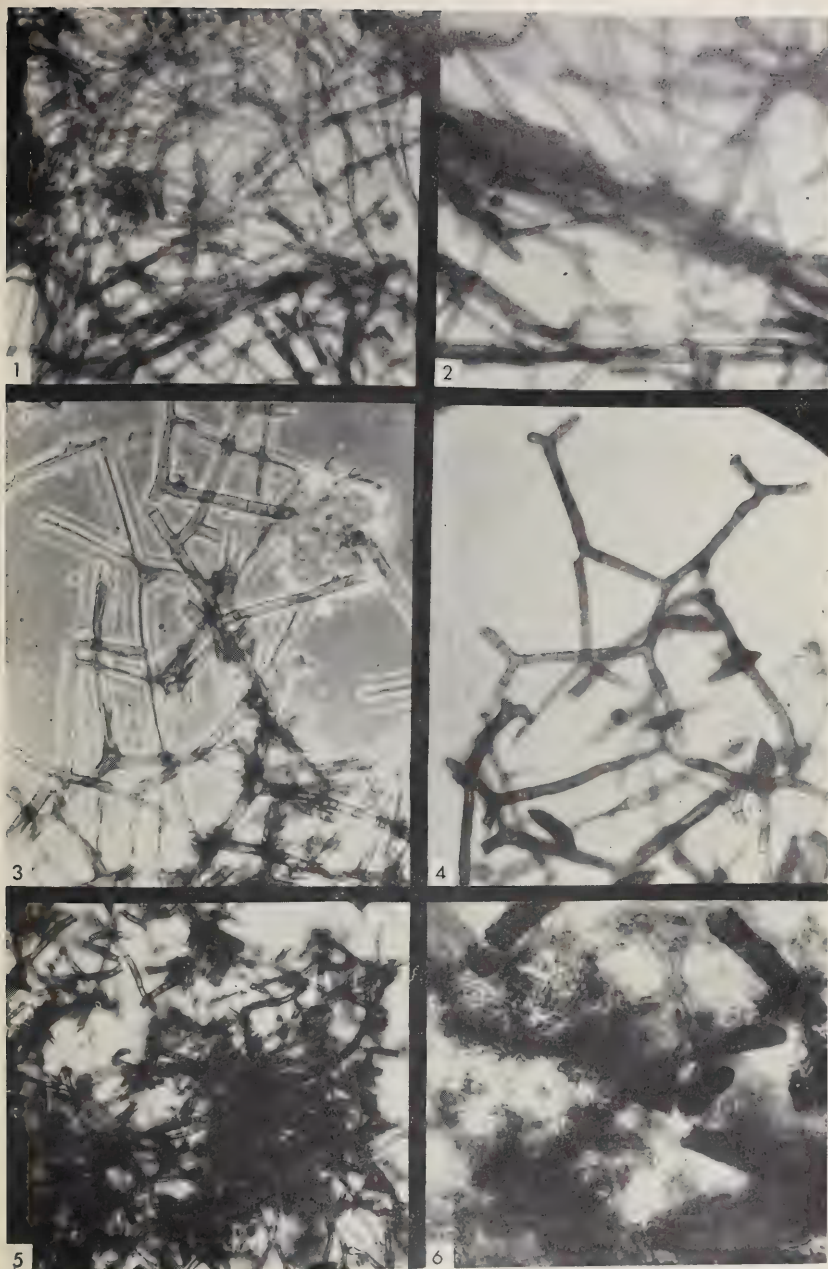


PLATE I.

Types of Subiculum in the Xylariaceae.

1. Loose and separable: *Xylaria euglossa*. $\times 470$.
2. Ropy: *Hypoxylon pulcherrimum* (*Rosellinia pulcherrima*). $\times 470$.
3. Reticulate: *Hypoxylon aquilum* (*Rosellinia aquila*). $\times 470$.
4. Reticulate-tentacular: *Hypoxylon cantareirens*. $\times 470$.
- 5 and 6. Closely anastomosed: *Hypoxylon corticium* (*Rosellinia corticia*). $\times 280$.

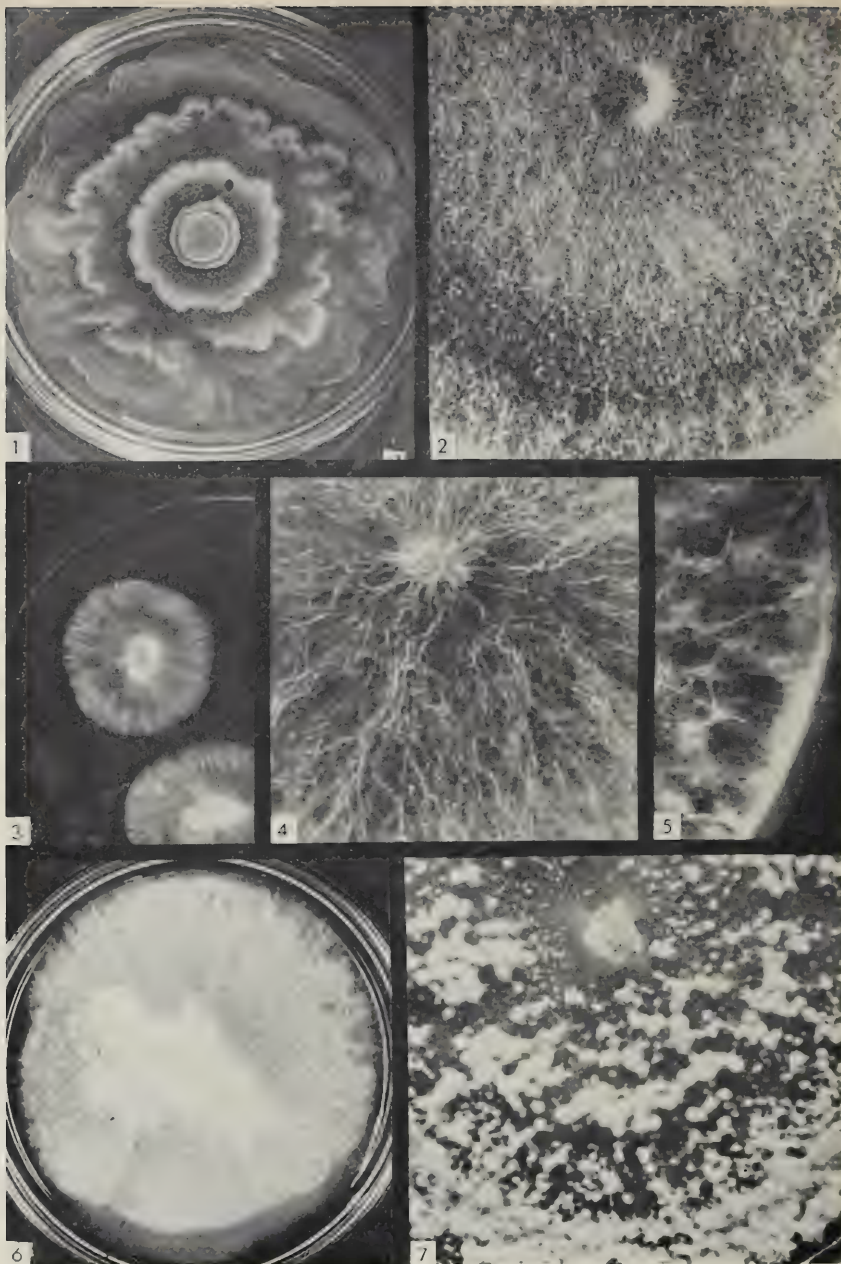


PLATE II.

Types of Colony in the Xylariaceae. I.

1. *Hypoxylon smilacicum*: zonate colony grading from submersed through canescent to appressed felty.
2. *Hypoxylon multiforme*: coarse felty type.
3. *Hypoxylon albocinctum*: young velvet colonies.
4. *Numulariola (Hypoxylon) tinctor*: cottony type with straggling hyphae.
5. *Numulariola mediterranea (Hypoxylon mediterraneum)*: cottony type with vertical tufts.
6. *Hypoxylon adumbratio* nov. sp.: gradation from velvety to lanose at centre.
7. *Xylaria cubensis*: floccose type.

stood. Dennis (1956, 1957), whose work provides some of the clearest illustrations of the Xylariaceae, still makes only brief mention of the types of tissue that occur. Miller (1928a) has partially analyzed the stromal layers in *Hypoxylon* and its close relatives but completely fails to homologise them with those of *Xylaria*.

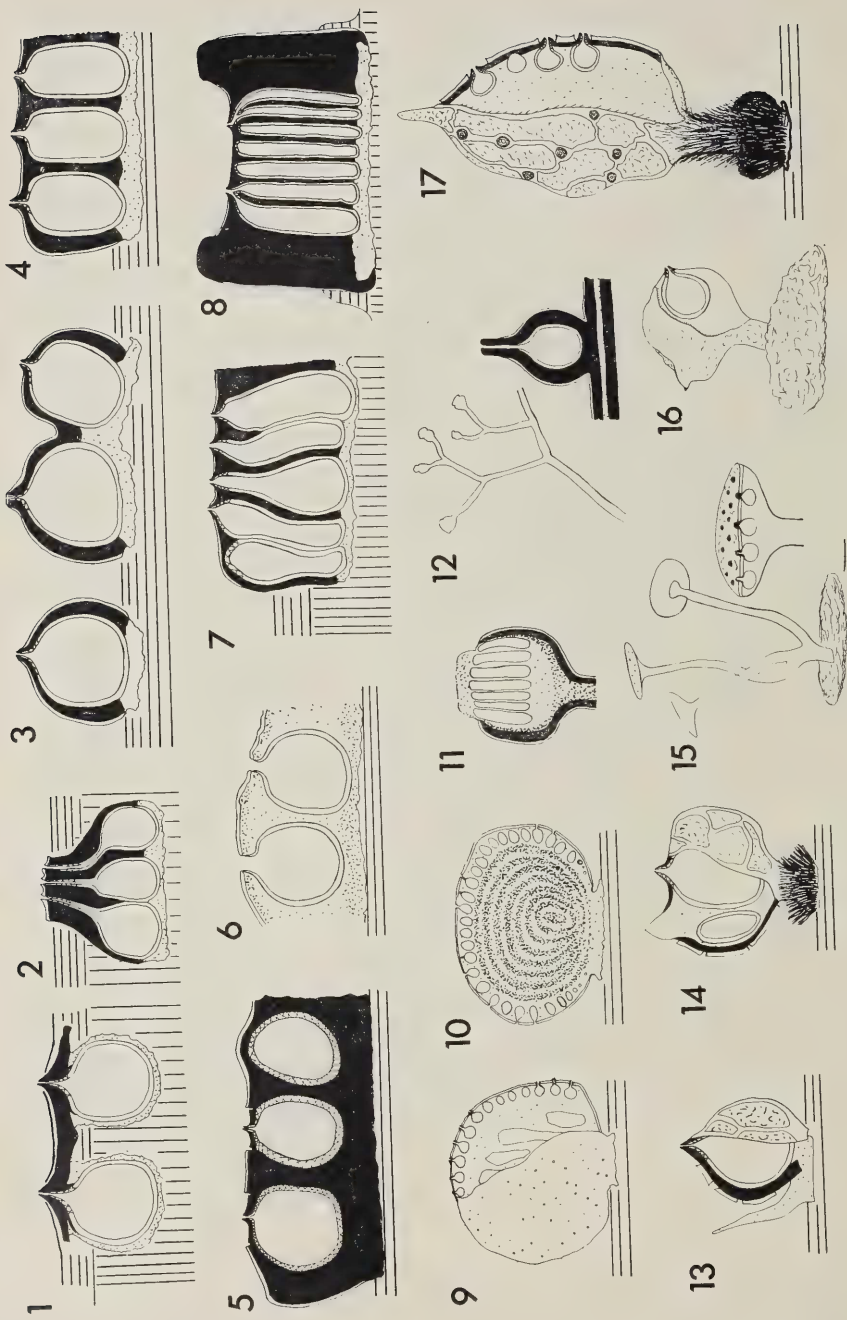
Two separate layers of the stroma were clearly recognized by him:

- (1) the "ectostroma" which is "that part of the stroma first formed in or on the periderm or on the bark when the wood has been removed, and functions in rupturing the bark when the latter is present; and which normally functions in producing the conidia", and
- (2) the "entostroma" which is "that portion of the stroma that develops under the ectostroma and bears the perithecia in its periphery". Miller's emendation of the genus *Hypoxylon* was based on the appearance and relative proportions of these two structures as defined.

In actual fact, while the conclusions drawn were mainly correct, he failed to recognize that there are actually *four* potential stromal layers each of which has useful taxonomic characters, and not all four are necessarily present together. Only the obscure tropical genera, *Phylacia* and *Thamnomycetes*, possess them all and give the clue to the correct homology of those remaining when one or more of those layers are absent. They comprise:

- (1) an outer veneer, usually coloured, that may be continuous, worn off irregularly, or remaining granulate;
- (2) an outer layer which is pale or coloured initially, and remains such or turns darker. This may be corky and persistent (as in *Xylaria*) or be composed of a brittle refractive coloured material (as in *Hypoxylon* section *Euhypoxylon*, and in *Phylacia*) that breaks up into small granules under microscopic examination. Initially it is continuous but later it may break up in a variety of characteristic ways, each one of specific value. This is the ectostroma, as the writer understands it, and is independent of conidial formation. It is not always developed, in which case the next layer becomes the outer one of the stroma;
- (3) a layer which is dark coloured, usually black and rigid, including deposits of carbonaceous material. It covers the perithecia or may enclose them as well;
- (4) an inner core, termed here as basal tissue, which is rarely carbonaceous, and is normally soft. This has been termed "fleshy" by most authors; the writer finds that this tissue varies in solidity, and the term "corky" is preferable when it is feebly resistant to the point of a needle. In colour it varies from white to dull brown or grey.

The two latter tissues form the structure known as the *entostroma*. No



separation occurs between them, and sectioning reveals continuity of tissue. On the other hand, layer (2) quite frequently separates from those underlying.

The double usage of the term "ectostroma" has resulted because layers (2) and (3) were considered identical. The nature of each layer is highly important generically, and their distribution for each genus is summarized in the following table. (See also Fig. I.)

LAYER	GENUS
1	<i>Hypoxylon</i> , sections <i>Annulata</i> and <i>Euhypoxylon</i> <i>Daldinia</i> <i>Phylacia</i> <i>Thamnomycetes</i>
2	All genera except <i>Podosordaria</i>
3	All genera except <i>Poronia</i> and <i>Podosordaria</i> , and <i>Hypoxylon</i> section <i>Euhypoxylon</i>
4	All genera except <i>Anthostomella</i> and <i>Lopadostoma</i> . Very poorly represented in the aplanate carbonaceous members of <i>Hypoxylon</i> section <i>Applanata</i> , <i>Nummularia</i> , <i>Bolinia</i> , <i>Camarops</i> , <i>Camillea</i> , <i>Theissenia</i> . and <i>Peridoxylon</i> .

10. *Perithecia*. The various shapes of perithecia have at some time been used to establish different genera, but it is hard to state objectively whether or not this is justifiable. Mere linear dimension is probably quite unreliable, as in the case of *Theissenia* which was erected primarily on large perithecial size.

FIGURE I. The Main Stromal Types in the Xylariaceae. (Not drawn to scale).

Diagrammatic representation:—

ectostroma—unaltered

carbonaceous entostroma—solid black

basal tissue of entostroma—stippled; intensity shows degree of discolouration

outer layer of substrate—horizontal lines

inner layer of substrate—vertical lines

1. *Anthostomella*
 2. *Lopadostoma*
 3. *Rosellinia*, uniperitheciate and
biperitheciate stromata
 4. *Hypoxylon*, section *Primocinerea*:
multiperitheciate
 5. *Hypoxylon* section *Annulata*
 6. *Hypoxylon*, section *Euhypoxylon*
 7. *Hypoxylon*, section *Applanata* & *Nummularia*
 8. *Camillea*
 9. *Entonaema*
 10. *Daldinia*
 11. *Phylacia*
 12. *Thamnomycetes*
 13. *Stilbohypoxyton*
 14. *Kretzschmaria*
 15. *Poronia*
 16. *Podosordaria*
 17. *Xylaria*
- } *Hypoxylon*, sect. *Entoleuca* (Syd.) Martin

The following types of perithecia occur and the writer would regard them as of specific rather than generic value:

<i>Perithecium</i>	<i>Orientation</i>	<i>Outline</i>	<i>Spacing</i>	<i>Arrangement</i>
Typical	Vertical	Globose to oval, longer than broad	Adjacent but not close crowded	Monostichous
Variants (not necessarily related)	Lateral (<i>Xylaria</i> , <i>Thamnomycetes</i>)	Conical, hemispheric; or tubular (<i>Camillea</i> , <i>Camarops</i>)	Well apart (<i>Rosellinia</i>) or close crowded (<i>Nummularia</i> , <i>Camillea</i>)	Polystichous (<i>Bolinia</i>)

11. *Ostioles*. The ostiole in the Xylariaceae merely refers conventionally to the entrance of the perithecium at the exterior of the stroma, but in practice the term includes the tissue immediately surrounding it. The formation of the ostiole is not a simple event, such as the cracking of the outer crust, but it is a definitely ordered process. In the majority of cases the details are hard to work out because of the large quantities of black material that obscure the sections. The following facts are evident, however:

- (a) the papillate ostiole, characteristic of the majority of the Xylariaceae with the hard rigid stromal layer (3), represents a localized development of the entostroma and becomes indistinguishable from the rest of it;
- (b) the truncate or annulate ostiole referred to by Miller (1961, pp. 9, 86 and elsewhere) is formed by the sloughing off of a circular plaque of the ectostroma around the ostiole, leaving it and part of the entostromal crust exposed. This occurs specifically in certain closely related species of *Hypoxylon* (the Annulate group) and intermittently through the rest of the Xylariaceae;
- (c) the umbilicate ostiole in noncarbonaceous species (*Hypoxylon*, section Euhypoxylon of Miller), represents another type of development in which the papillate portion described above is deliberately released, leaving a pore that is often circumscribed and usually periphysate. Umbilicate ostioles also occur in carbonaceous species of the Applanata section of *Hypoxylon*. In some (*H. tinctor*) they are apparent simply because the ectostroma overlies the carbonaceous layer and when worn away will expose normal papillate ostioles, while in others (*H. punctulatum*) the carbonaceous layer simply appears not to form a protrusion.

The close correlation of the ostiole development with stromal type makes its character, when interpreted correctly, of major value in classification.

12. *Asci*. The structure of the ascus is another feature little investigated. That it is basically unitunicate was determined by Luttrell (1951, p. 58) and

presumably confirms the advanced position of the Xylariaceae. The most interesting part is, however, the amyloid "ascal plug", stainable by iodine, which is mentioned frequently in the specific diagnoses of Saccardo (1882, et seq.), Dennis (1956, 1957) and Carroll (1963). The structure is rectangular, cubic, discoid, or flattened, rarely absent, and differentiates early in the development of the ascus at the apex of the ascospore column. Although the plug is longitudinally cleft in the centre, the ascospores bypass it during dehiscence, so that the function, if any, is vague. Taxonomically, since there is a good correlation between the shapes just listed and other characters especially stromal ones, it should be regarded as a major criterion.

TYPE OF ASCAL PLUG	GENUS
(1) None at all	<i>Hypoxylon</i> section Euhypoxylon
(2) Flattened disc (Fig. II, 9)	<i>Lopadostoma</i> <i>Hypoxylon</i> subsection Papillata sections Annulata and Euhypoxylon <i>Daldinia</i> <i>Phylacia</i> <i>Thamnomycetes</i> <i>Entonaema</i> <i>Hypoxylon</i> section Applanata <i>Camarops</i> <i>Nummularia</i> <i>Bolinia</i> <i>Theissenia</i> <i>Peridoxylon</i> <i>Camillea</i>
(3) Broader than high (Fig. II, 10)	<i>Anthostomella</i> <i>Rosellinia</i> <i>Hypoxylon</i> subsect. Primocinerea <i>Hypoxylon</i> section Applanata <i>Penzigia</i> <i>Stilbohypoxydon</i> <i>Kretzschmaria</i> <i>Xylaria</i> <i>Poronia</i> <i>Podosordaria</i>
(4) Cubic to Rectangular (Fig. II, 11)	<i>Rosellinia aquila</i> and related species <i>Xylaria</i>
(5) Similar to (4) but with rounded lower end and a constriction below the upper end (Fig. II, 12)	

Other features of minor importance are the ascal shape, thickness of wall, duration after maturity, number of spores (8, rarely 4), arrangement of spores, the ratio of fertile to sterile portion (stipe), and the absolute size.

13. *Spore size.* Of all the characters, size has been considered paramount in mycological literature. Miller (1961), in fact, uses it to segregate most of his species. The writer has found that some species groups, (*Kretzschmaria* and the Applanata section of *Hypoxylon*) contain some members with very long spores, but that otherwise spore dimensions are of no generic value. Furthermore the value of spore sizes for specific destination is diminished by:

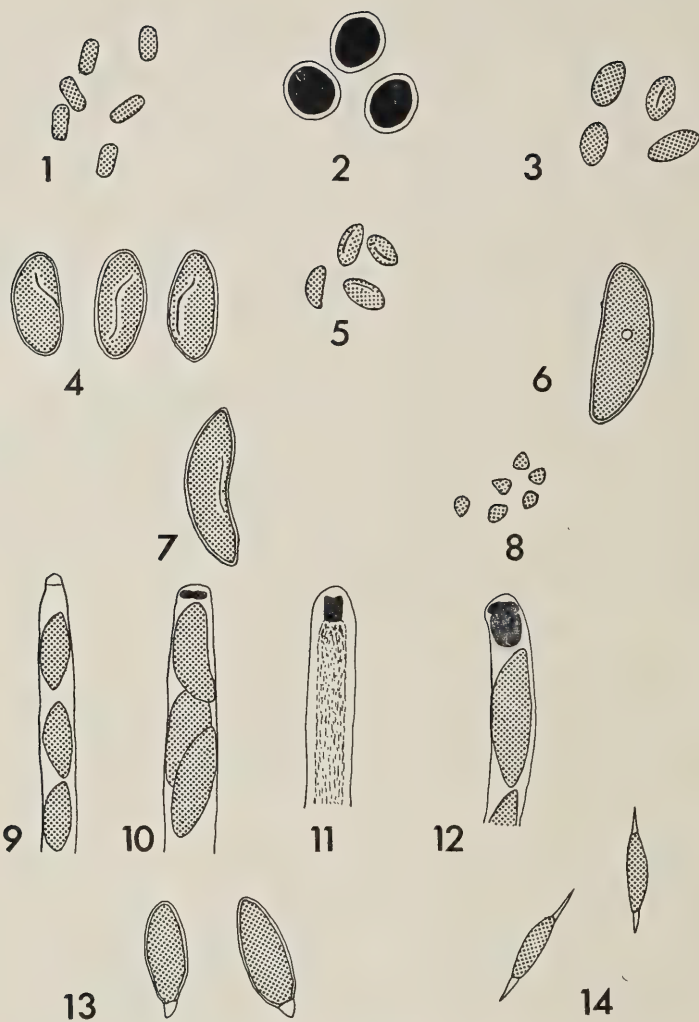


FIG. II. Types of Asci and Spores and their characters.

1. *Phylacia surinamensis*: globose spores with parallel sides. 2. *Numulariola (Nummularia) discreta*: globose spores with thick hyaline sheaths. 3. *Hypoxylon mastoideum (Rosellinia mastoidea)*: oval equilateral spores. 4. *Xylaria longipes*: Oval—elliptic, gibbous spores with spiral germ slit on the less convex sides. 5. *Hypoxylon rubiginosum*: navicular spores with straight germ slits on the convex sides. 6. *Numulariola (Hypoxylon) divergens*: navicular spore with poroid germ slit. 7. *Xylaria polymorpha*: broad crescentic spore with straight germ slit on the concave side. 8. *Numulariola polysperma (Camarops polyspermum)*: spores with one end conical. 9. *Lopadostoma (Anthostoma) turgidum*: ascus with very thin apical plug. 10. *Hypoxylon rubiginosum*: ascus with discoid plug. 11. *Anthostomella nitidissima*: young ascus with rectangular plug. 12. *Hypoxylon pulcherrimum (Rosellinia pulcherrima)*: ascus with constricted plug. 13. *Anthostomella sabalensioides*: spores with a hyaline apiculus on the proximal end. 14. *Hypoxylon thelenum (Rosellinia thelena)*: spores with acicular apiculae.

- (a) the great range, especially for length, within a single sample;
- (b) the occurrence, though infrequent, of two separate sizes within the same stroma (*Hypoxylon rubiginosum*);
- (c) the frequent disparity in spore sizes between different collections of otherwise similar stromal material.

In the majority of the Xylariaceae, the average spore lengths are less than 15μ ; but the entire range extends from 2 up to 100μ . One might regard small differences between the smaller spores as having greater value than those between larger spores, or one might give equal weight to equal intervals, but either case involves subjective interpretation and it is not easy to find mathematical formulae to cover all possibilities. For the present, the writer has accepted differences of 2μ in the spore average between samples as indicating separate specific rank, but only when they are allied with differences in the major characters.

14. *Spore shape*. The spores fall into six definite categories, although there are usually intergrades in each sample:

- (a) equilateral with sides parallel (cylindric); *Camillea*, *Phylacia*, *Thamnomycetes*; (Fig. II:1)
- (b) equilateral, side convex (globose to elliptic); All genera; (Fig. II:2, 3)
- (c) inequilateral, sides convex (gibbous); All genera; (Fig. II:4)
- (d) one side convex, the other flat (navicular); All genera except in *Camillea*, *Phylacia*, *Thamnomycetes*; (Fig. II:5, 6)
- (e) one side convex, the other concave (broad crescentic); Section *Applanata* of *Hypoxylon*, and *Xylaria*, and *Kretzschmaria*; (Fig. II:7)
- (f) semi-triangular; *Camarops*; (Fig. II:8)

Spore shape can only be used on a specific level but its main interest lies in the fact that there is a clear if incomplete association of elongate navicular or crescentic spores with those species of *Penzigia*, *Kretzschmaria* and *Xylaria* in which the stroma contains white basal tissue and a similar prevalence of short oval to elliptic spores in other species. Certain species groups (Miller's section *Euhypoxylon* of *Hypoxylon*, and the genus *Daldinia*) contain no elongate spores at all. When more is known about the tropical species, further analysis of these characters will prove interesting.

15. *The germ slit*. There are three types that can be distinguished: elongate straight, (Fig. II:3, 5) elongate spiral, (Fig. II:4) and poroid, (Fig. II:6). The first can occur on the concave or convex sides of inequilateral spores, the second on the concave side only, and the third apparently anywhere on the spore. The interest of this lies in the restriction of the spiral type to some species within *Rosellinia*, *Penzigia*, *Kretzschmaria* and *Xylaria*; which is, incidentally, the same generic distribution as for the subiculum. In addition, all the latter three genera have the germ slit on the concave side of inequilateral spores and the same is

true for the majority of inequilateral spores in *Rosellinia*. The value of the character is limited only by the fact that it is impossible to know at present which side of the equilateral spores corresponds to the flat-sided or concave one of the inequilateral spores so that no general homology covering all spores may be made.

16. *Spore sheath*. This character lends weight to the validity of some of the established taxa but its inconstancy prevents it from being used to differentiate absolutely between them.

- (1) No sheath recognisable

Hypoxyton, sections:

Euhypoxyton

Papillata

Applanata

Nummularia and allied genera

- (2) Sheath distinct:

Anthostomella

Lopadostoma

Rosellinia spp. with dark subiculum

Hypoxyton subsection *Primocinerea*, part

Kretzschmaria

Xylaria and allied genera

- (3) Sheath very prominent: (Fig. II:2)

Nummularia discreta

Podosordaria spp.

17. *Spore apiculus*. (Fig. II:13, 14) Though apparently continuous with the spore sheath and of the same substance, the distribution of apiculae throughout the family follows a different pattern from that of the spore sheath. Apiculae are characteristic of *Anthostomella*, part of the section *Applanata* of *Hypoxyton*, and are occasionally found in *Rosellinia* and *Xylaria*. They are usually short and are borne on one or both ends of the spore. Rarely are they acicular as in *Rosellinia thelena*. The apiculae provide good specific characters, but unfortunately they frequently disappear after maturity.

B. Cultural characters.

The following information is based on the culture of some 600 strains of the Xylariaceae. The most significant results were obtained when malt agar was used as the culture medium.

18. *General macroscopic growth characters*. No culture type was found exclusively for any species group based on stromal characters. Submersed, canescent or velvety types, usually not producing stain, occurred throughout. The following table shows the most important correlations, descriptions being

based on 14-day-old plate cultures grown on malt agar. For terms applicable to the mycelium the writer has used the definitions provided by Long and Harsch (1918).

TYPE	FOUND IN
(1) Colonies submersed to canescent, smooth dull white, hyaline or subhyaline; conidial formation usually profuse and rapid, or else absent entirely; stain absent or slight. Conidia fawn to grey, growth slow to moderate (0—4.0 mm per day at 25°C).	<i>Anthostomella</i> (part) <i>Rosellinia</i> (part) <i>Hypoxylon</i> subsect. <i>Primocinerea</i> (part) (Plate III:2) <i>Hypoxylon</i> sect. <i>Euhypoxylon</i> (part)
Conidia red brown or orange brown, growth variable.	
(2) Colonies silky with smooth strands overlaying a felty interior; white, but often with "carbonization" of the medium present in small oval patches at the base of the colony with age; stain absent; growth rapid (>4.0 mm per day at 25°C).	<i>Rosellinia necatrix</i> and close relatives
(3) Colonies velvet felty to fleecy uniform or zonate, white, subhyaline to opaque, usually smooth; "Carbonization" of the medium often present; stain absent; growth moderate to slow (0—4.0 mm per day at 25°C).	<i>Anthostomella</i> (part) <i>Hypoxylon</i> subsect. <i>Primocinerea</i> (part) (Plate II:1, 3, 6; Plate III:5)
(4) Colonies velvet to fleecy or floccose, rough or smooth, uniform or zonate, sometimes plumose, normally with pronounced tendency to coremial formation; carbonization of the medium usually very marked; stain none; growth moderate (2.0 mm/day—4.0 mm/day).	<i>Kretzschmaria</i> <i>Penzigia</i> <i>Xylaria</i> <i>Poronia</i> <i>Podosordaria</i> (Plate II:7; Plate III:6; Plate V:1—3)
(5) Colonies velvet felty, dull white or variously coloured, subhyaline or opaque, surface smooth or coarse; carbonization rare; stain usually pronounced, some shade of amber, ochre yellow, red-brown, red or violet; growth moderate (>2.0 mm/day) to fast (>4.0 mm/day).	<i>Hypoxylon</i> , subsect. <i>Papillata</i> section <i>Annulata</i> <i>Phylacia</i> <i>Daldinia</i> (Plate II:2)
(6) Colonies coarse felty or cottony, rarely somewhat velvety, dull white or variously coloured, subhyaline to opaque, carbonization absent; stain flecked or uniform, ochre yellow to red-brown or olive green, usually pronounced. Growth rate rarely below 4.0 mm/day. Secondary mycelium tentacular; surface infrequently showing ropy or straggling hyphae and vertical tufts of mycelium. Secondary mycelium otherwise; surface usually with ropy or straggling hyphae and vertical tufts of mycelium.	<i>Hypoxylon</i> sect. <i>Euhypoxylon</i> (part) (Plate III:4) <i>Daldinia</i> <i>Hypoxylon</i> sect. <i>Applanata</i> <i>Nummularia</i> (Plate II:4 and 5; Plate III:3)

No information is available for *Lopadostoma*, *Bolinia*, *Camarops*, *Camillea*, *Peridoxylon*, *Theissenia*, *Entonaema*, *Thamnomycetes* or *Stilbohypoxyton*. How-

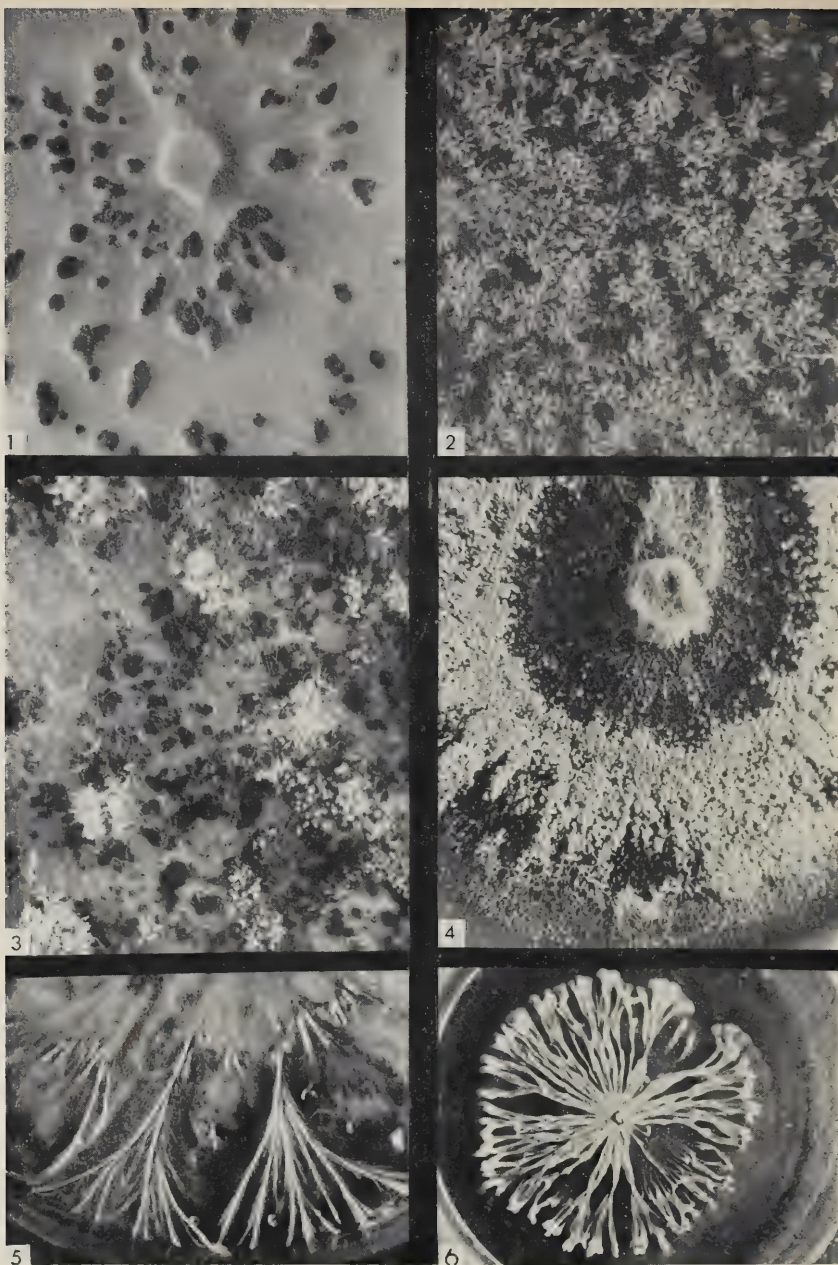


PLATE III.

Types of Colony in the Xylariaceae. II.

1. *Hypoxylon thelenum* (*Rosellinia thelena*): silky mycelium overlaying small carbonaceous areas in fleck formation through the substrate.
2. *Hypoxylon serpens*: canescent mycelium with rapid conidial formation.
3. *Daldinia concentrica*: coarse felty mycelium with dark mycelial aggregates of tentacular mycelium close to substrate level.
4. *Hypoxylon rubiginosum*: felty mycelium with light coloured mycelial aggregates.
5. *Hypoxylon mastoideum* (*Rosellinia mastoidea*): showing plumose hyphae at margin of colony.
6. *Xylaria cornu-damae*: velvet colony with plumose development.

ever this table quite clearly shows broad differences in behaviour between species groups defined on stromal characters. It reinforces the traditional concept, derived from study of perfect stages only, that there are gross affinities between the superficial colourless genera comprising *Xylaria* and its allies on the one hand, and between the genera with an outer pigmented layer on the other. There is, however, a small overlap between the two.

19. *Mycelium*. The primary mycelium shows little in the way of exceptional characteristics. However there does not appear to be correlation between diameter, degree and spread of the marginal hyphae, and the growth rate. The majority of species have growth rates slower than 4 mm/day and hyphae which are close packed and less than 3 mm diameter, while a small number of species in *Daldinia* and in the section *Applanata* of *Hypoxylon* have faster growth rates and widely spread "pioneer" hyphae of at least 3 mm diameter. The dark-subiculate species of *Rosellinia* on the other hand are fast growers, but may have narrow marginal hyphae.

The secondary mycelium which develops as the colony matures, is more interesting in its variation. Five basic types exist altogether in the Xylariaceae, which show direct resemblance to the subicular types of mycelium occurring in nature that have already been described (p. 10). The ropy type (2) is the most common. In contrast to the first four types of mycelium however, the fifth type is infrequent in the field, while in culture it is characteristic of *Daldinia* and of 3 species in *Hypoxylon* sect. *Euhypoxylon*: *H. subchlorinum*, *H. howeianum* and *H. sclerophaeum*. This incidentally confirms the affinity already noted between the two genera.

In some cultures certain characteristic structures develop with age that may be termed *mycelial aggregates*. These are cushion-shaped or spherical pads of mycelia chiefly composed of secondary mycelium when mature though largely primary at first. They occur in all cultures of *Daldinia*, sporadically in *Hypoxylon* sections *Euhypoxylon*, *Annulata* and *Papillata*, and occasionally in the section *Applanata* (*Hypoxylon mediterraneum*).

Further inspection of the cultures also showed that:

- (a) secondary mycelium was absent from species of *Anthostomella* and absent or weakly developed (type 1) in *Rosellinia* and *Primocinerea*;
- (b) the type of mycelium in the stromal subiculum may not always agree with that formed in culture by the same strain. Hence it is difficult to decide how fundamental the differences in mycelial development are.

20. *The Imperfect stage*. The imperfect stages of the Xylariaceae have only been sporadically described in the literature and never made use of in classification. It is difficult to account for this lack of observation because conidia are often easy to find developing freely or in coremia on the surfaces of most

developing stromata, or in close association with them. The earliest mention of a conidial stage is that of Persoon (1808) in his description of *Isaria umbrina*, associated with *Hypoxylon fragiforme*. With few exceptions, the later writers only concerned themselves with the dark-subiculate species in *Rosellinia* which contain many pathogens of economic importance such as *R. necatrix* (Berlese, 1892; Brooks, 1953; Hansen, Thomas, and Earle 1937; Hartig 1883, 1894; Prilleux, 1904), *R. quercina* (Hartig, 1880) and *R. radiciperda* (Massee, 1896), with *Nummularia discreta* (Gloyer, 1921; Hasselbring, 1902), with *Hypoxylon deustum* (sub *Ustulina*: Brooks, 1915; Petch, 1912, 1921, 1923; Wilkins, 1936, 1938, 1939) and with various species of *Xylaria* (Brown, 1913; Fromme, 1928; Guéguén, 1906, 1907, 1909; Petch, 1907, 1913, 1927). The chief attempts to combine conidiophore and conidial morphology with that of the stroma for a large number of species are those of Jaczewski (1896, pp. 110–136) and Traverso (1906, pp. 31–172).

In the present investigation the number and variety of conidiophore types have been found sufficiently large to be of significant value in the delimitation of species and even genera but their contribution to the overall picture is diminished by two disadvantages:

- (a) not all stromata, even when collected at or after maturity, will germinate on malt agar or on more complex synthetic agars and a sizeable minority of those that do, still fail to fruit;
- (b) two or more types of conidiophore and/or cultural type may belong to stromal forms which resemble each other very closely.

The variation in linear measurements of various characters also may vary so greatly that it is difficult to determine which are really significant. If all the available characters from both perfect and imperfect stages were given equal weight it would often be very hard to draw specific distinctions among samples between which there is apparently equal taxonomic distance.

The following table shows the distribution of the conidiophores for 95 species of the Xylariaceae. *Hypoxylon* is somewhat over-represented due to the greater ease of obtaining conidiophores in culture, while *Nummularia*, *Bolinia*, *Lopadostoma*, *Phylacia* and *Thamnomycetes* are poorly represented for the opposite reason. No fresh material for culturing was available for *Entonaema*, *Camarops*, *Theissenia*, or *Stilbohypoxyton*. The fractions of the species total and the same expressed as a percentage are figured in each column.

The distribution of conidiophore types in such a definite arrangement can hardly be ascribed to chance, and there does appear to be a reasonable correlation with stromal characters. Perhaps the most interesting feature is the distribution of coremial types. The "ropy" type occurs, though in small numbers, throughout the dark-subiculate members of *Rosellinia* and the sections Papillata

Correlation of Conidiophore Types with the Genera of the Xylariaceae (as traditionally defined)

Genus or Subsection		Types of conidiophore											
		Basidio-botrys			Acrostiaphyllus			Sporothrix			Nodulisporium		
Genus or Subsection	No. of Species	Type I			Type I			Type I			Type I		
		Type II			Type II			Type II			Type II		
Anthostomella	4/4	0	0	0	0	0	0	0	0	0	3/4	1/4	0
Lopadostoma	100	0	0	0	0	0	0	0	0	0	75	25	0
Rosellinia	5/12	0	0	0	0	0	0	0	0	0	12/12	0	0
* Hypoxylon	13/13	0	0	0	0	0	0	0	0	0	9/13	4/13	0
subsect. Primocinerea	100	0	0	0	0	0	0	0	0	0	69	31	0
Hypoxylon	2/4	0	0	0	0	0	0	0	0	0	0	0	0
subsect. Papillata	100	0	0	0	0	0	0	0	0	0	4/4	0	0
Hypoxylon	4/4	0	0	0	0	0	0	0	0	0	0	0	0
section Annulata	100	0	0	0	0	0	0	0	0	0	0	0	0
Hypoxylon	3/25	0	0	0	0	0	0	0	0	0	8/25	0	0
section Euhypoxylon	100	0	0	0	0	0	0	0	0	0	3/5	0	0
Daldinia	5/5	0	0	0	0	0	0	0	0	0	1/5	0	0
Entomacra	—	—	—	—	—	—	—	—	—	—	—	—	—
Phylacia	—	—	—	—	—	—	—	—	—	—	—	—	—
Thamnomycetes	11/11	0	0	0	0	0	0	0	0	0	1/11	0	0
Hypoxylon	100	0	0	0	0	0	0	0	0	0	9	0	0
section Appianata	100	0	0	0	0	0	0	0	0	0	18	0	0
Nummularia	2/2	0	0	0	0	0	0	0	0	0	0	0	0
Camtrops	—	—	—	—	—	—	—	—	—	—	—	—	—
Thelissenia	—	—	—	—	—	—	—	—	—	—	—	—	—
Camillia	—	—	—	—	—	—	—	—	—	—	—	—	—
Bolivia	—	—	—	—	—	—	—	—	—	—	—	—	—
Kretzschmaria	0	0	0	0	0	0	0	0	0	0	0	0	0
Stilbohypoxyton	1/3†	0	0	0	0	0	0	0	0	0	1/3†	0	0
No. of Species	—	—	—	—	—	—	—	—	—	—	—	—	—
Penzigia	33	0	0	0	0	0	0	0	0	0	33	0	0
%	1/3	0	0	0	0	0	0	0	0	0	1/3	0	0
Xylaria	33	0	0	0	0	0	0	0	0	0	11	0	0
No. of Species	—	—	—	—	—	—	—	—	—	—	—	—	—
Poronia	0	0	0	0	0	0	0	0	0	0	0	0	0
No. of Species	—	—	—	—	—	—	—	—	—	—	—	—	—
Podosordaria	1/3	0	0	0	0	0	0	0	0	0	1/3	0	0
%	1/3	0	0	0	0	0	0	0	0	0	1/3	0	0

* Includes *H. densum*, to be transferred to *Kretzschmaria*
† *Penzigia discolor*, to be transferred to *Hypoxylon* (Entoleuca: Primocinerea)

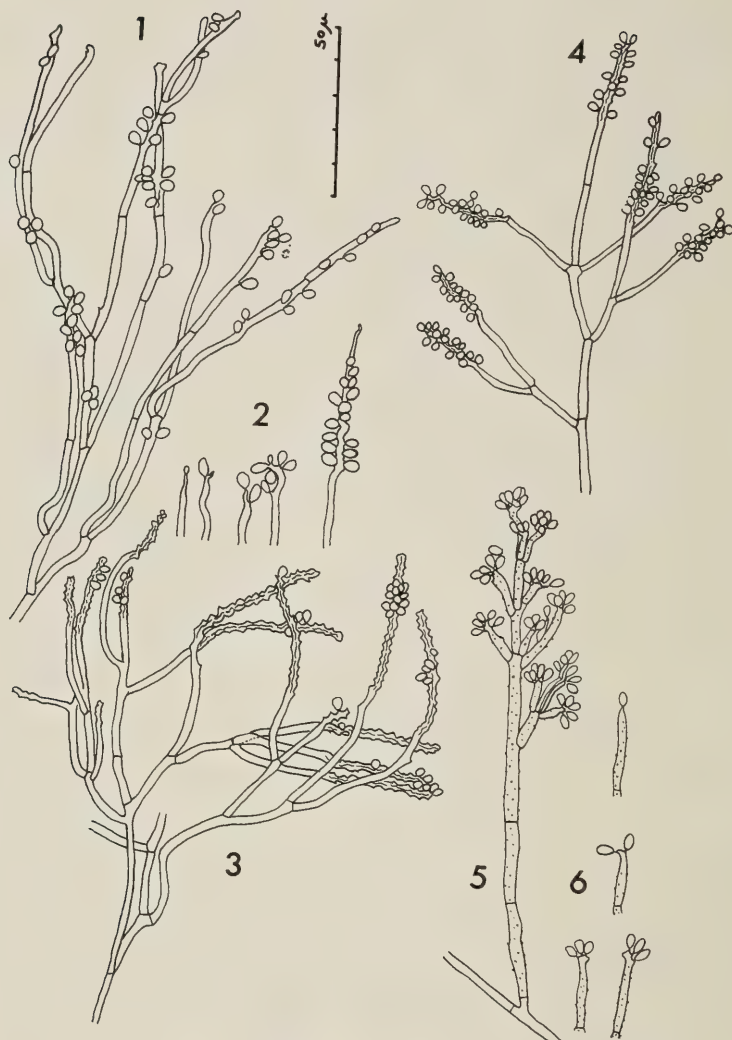


FIG. III. Conidiophores in the Xylariaceae. I.

1. *Hypoxylon albocinctum*: *Nodulisporium* type I. 2. *Hypoxylon albocinctum*: showing development of the conidia. 3. *Anthostomella melanotes*: *Nodulisporium* type II. 4. *Hypoxylon* (*Rosellinia*) *mastoideum*: *Nodulisporium* type II with predominantly ternate branching. 5. *Hypoxylon truncatum*: *Acrostaphylus* type I. 6. *Hypoxylon truncatum*: showing development of the conidia. Compare with 2.

and Euhypoxylon of *Hypoxylon* (Plate IV:1-5). These are minute, not exceeding 4 mm in length, and are composed of dark uniform hyphae more or less parallel or coiled, bearing conidiophores at the surface. No differentiation takes place between the inner and outermost hyphae and the coremia remain short aristate, though sometimes connected together at the base, as in *Hypoxylon fragiforme*. The "fleshy" type is characteristic of *Kretzschmaria*, *Xylaria*, *Poronia* and *Podosordaria*, and is usually larger in size, extending up to 6 cm (Plate IV:6; Plate V:1-6). There is usually a distinct resemblance towards the structure of the stroma in species of *Xylaria* in that an outer layer of dark intertwined hyphae, sometimes impregnated with rigid "carbonaceous" material, is differentiated from an inner white fleshy core. The base of the coremium often bears long brown setose hyphae, the middle section is usually glabrous, grey, black, or white, while the apex may remain white or flesh-colour or develop a "collar" tinted white, yellow or orange. The smaller coremia, below 15 mm high, often lack the central grey-black section and are more or less uniformly pale. The fleshy coremia are by no means necessarily fertile; repeated culturing of many Xylarias seems to indicate that sterility may be normal, or the period of formation of conidiophores to be long delayed. Conidia, when developed, occupy the apex or sides of the coremium or both, and tend to obscure the features described above. In the large members of *Xylaria*, particularly in coremia grown in the field, the conidiophores are parallel, forming a palisade, but outside these the conidiophores are randomly orientated and easily separable for examination.

The coremium of the Xylariaceous groups of genera probably represents the initial stages of the stroma in most cases, perithecia later developing below the conidial region. Yet this too is not obligatory, since many withered coremia can often be found in the field associated with mature stomata. As in the rest of Xylariaceae, no coremial culture has yet given rise to stomata under laboratory conditions, whether on wood or agar. The formation of stomata obviously requires some subtle factor or principle not yet understood.

Classification of the Imperfect Stages

This is a difficult task because the imperfect form genera themselves overlap in concept, and are often not capable of precise definition. The fungi show wide variations, often within the same sample, in total length, degree of branching and arrangement of the branches, and also a certain variation in degree of colouration. All these characters are classically adopted in the division of the Fungi Imperfecti.

The coremia, which are classified mainly on external morphology, can be assigned to the genera *Graphium* (ropy type) and *Isaria* (fleshy type). Several



FIG. IV. Conidiophores in the Xylariaceae II.

1. *Hypoxylon rubiginosum* and *H. oodes*: *Sporotrichum* type I. 2. *Hypoxylon fuscum*: *Sporotrichum* type I, also with conidia in fascicles off the sides of the hyphae. 3. *Hypoxylon investiens*: *Sporotrichum* type II. 4. *Hypoxylon aureostroma* sp. nov. (Section Euhypoxylon): *Sporotrichum* type III. 5. *Hypoxylon hypomiltum*: *Sporotrichum* type IV. 6. *Hypoxylon murcidum*: *Sporotrichum* type V. 7. *Xylaria digitata*: *Sporotrichum* type V. 8. *Hypoxylon rubrostromaticum*: *Acrostaphylus* type I. 9. *Xylaria ianthino-velutina*: *Acrostaphylus* type II.

authors, notably Brooks (1953), Lloyd (1916, 1917a, 1917b, 1918, 1923a, 1923b) and Petch (1910, 1923) have recognised this connection. Traverso (1906, p. 172) has also reported and figured an acervular type of fruiting body for *Lopadostoma* (sub *Anthostoma melanotes*), somewhat similar to *Cytospora*, but this remains to be confirmed.

The conidiophores of the Xylariaceae can be divided into three fairly distinct types based on method of origin of the conidia and the degree of distinction of the conidiophore from the vegetative mycelium.

1. *Nodulisporium* Preuss. (Fig. II:1-4). The conidiophores are usually very long, lax, much branched, often exceeding 500μ . The structures may not be easily differentiated from the vegetative mycelium because the hyphae are alike in diameter. The conidia arise laterally and apically off the sides of the fertile branches, the tip of which bends away from the point of origin of each spore before giving rise to the next one. This bending takes place in one or more planes but the net effect is a characteristic geniculate pattern with the conidia remaining attached in the notches along the fertile branch. The fertile branch may only start fruiting late in its development, in which case the conidial area will be short, or it may fruit throughout much or nearly all of it. The writer considers the latter condition to be the most primitive since it is accompanied by the least degree of differentiation, and is therefore designated type I, and the other as type II. We can also recognise two forms within the second type, those with dichotomous branching (IIa) and those with ternate branching (IIb), but the distinction is not sufficiently consistent between species to be useful.

The conidia are one-celled, subglobose to long clavate, with the distal end narrow or broad-rounded and the proximal distinctly truncate due to the wide area of attachment. The colour varies from white to deep grey or fawn brown, not being as diverse as the types to follow.

The *Nodulisporium* stage is characteristic of *Anthostomella*, *Rosellinia*, and the Primocinerea subsection of *Hypoxylon*, and it occurs sporadically in *Daldinia*, *Penzigia*, *Xylaria* and *Podosordaria*. There is no major difference in form between any of these apart from the distribution of the conidia, and both types defined above are universal. The correlation with the stroma type is therefore a rather wide one.

2. *Sporothrix* Hektoen & Perkins (1900). (See also Carmichael, 1962). The conidiophores vary from very long to extremely short and are unbranched or indefinitely ramose and penicillate, but they are always the same diameter as the vegetative mycelium and smooth-walled. (Fig. IV: 1-6, 8). The conidia are shortly pleuracrogenous or are borne almost at the same level at the apex, with the oldest near the base and the youngest in the centre. If the apex continues growth after fruiting, the conidia are left behind as a fascicle, or very rarely



FIG. V. Conidiophores in the Xylariaceae III.

1. *Hypoxylon sclerophaeum*: *Acrostaphylus* type II. 2. *Hypoxylon haematostroma*: *Acrostaphylus* type II. 3. *Numulariola nummularia* (*Hypoxylon nummularium*): *Acrostaphylus* type II. 4. *Numulariola mediterranea* (*Hypoxylon mediterraneum*): showing variation in *Acrostaphylus* types. 5. *Numulariola* (*Hypoxylon*) *tinctor*: simple *Acrostaphylus* type I. 6. *Numulariola* (*Hypoxylon*) *tinctor*: showing development of the compound *Basidiobotrys* conidiophore. 7. *Numulariola* (*Hypoxylon*) *tinctor*: mature, typical, compound *Basidiobotrys* type. 8. *Numulariola punctulata* (*Hypoxylon punctulatum*): *Basidiobotrys* type. 9. *Numulariola mediterranea* (*Hypoxylon mediterraneum*): *Basidiobotrys* type. 10. *Numulariola mediterranea* (*Hypoxylon mediterraneum*): *Acrostaphylus* type associated with above.

singly. The fertile branches are never geniculate, and the conidia are sessile or attached by a broad or narrow sterigma. Due to this variation, the proximal end may be narrow truncate, rounded or acuminate, and the shape correspondingly varies from clavate to oval or elliptic to napiform and pyriform. The colour varies between white, grey, yellow, pink, fawn-brown, red-brown and dull-brown.

The *Sporothrix* type can be subdivided into a number of intergrading variants on the degree and type of branching:

- I. unbranched and usually short; *Hypoxylon* sect. Euhypoxylon;
- II. branched to the first or second degree or indefinitely; branching mainly dichotomous but sometimes with sporadic verticils.

<i>Hypoxylon</i>	{	subsect. Papillata sect. Euhypoxylon sect. Applanata (occasional)
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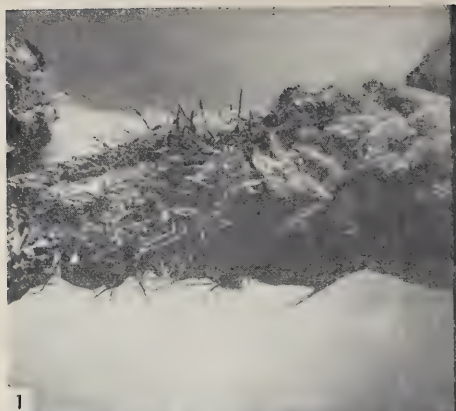
Daldinia
Xylaria
Poronia

- III. apparent axes sparingly branched, with long fertile axes along which the conidia are clustered in repeated fascicles or off short terminal hyphae; branching is sympodial, and the verticils or terminal hyphae represent the ends of successive main axes: *Hypoxylon* sect. Euhypoxylon only;
- IV. with the majority of branching ternate and the ends of the branches swollen into a distinct globose flaring head; the branches are aligned with the main axis to resemble a trident: *Hypoxylon* sect. Euhypoxylon only;
- V. with the majority of branches verticillate, 3-6 branches per node, resembling *Calcarisporium*: *Hypoxylon* sect. Euhypoxylon, and *Xylaria*.

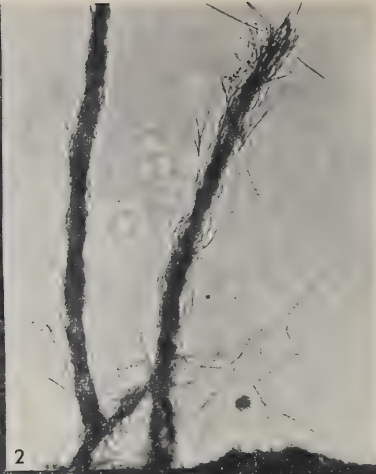
3. *Acrostaphylus* Arnaud ex Subramanian (1956). (Fig. III:5 and 6; Fig. IV:8 and 9; Fig. V). The conidiophores are of the same general plan as in *Sporothrix* but differ in that the axis is well defined, with the branches usually over the upper half only, and the fertile branches and axes are stout in relation to the vegetative mycelium. Warty walls and an amber, yellow, brown or purplish tint are further characteristic but inconstant features. Subramanian (1956, p. 482) clearly regards the genus as belonging to the Dematiaceae, but this is doubtful as the conidia are always light coloured and the conidiophores rarely opaque. The conidia are similar in form and method of origin to those of *Sporothrix*.

The series can be divided into four groups though again there are many intergrades:

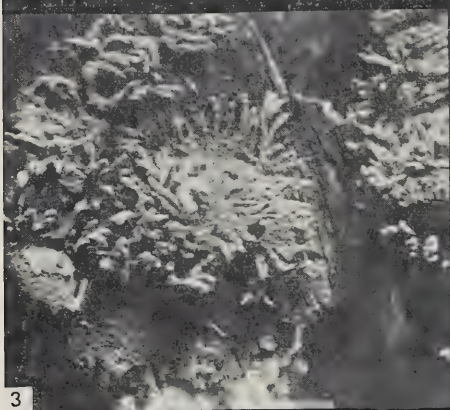
- I. conidiophores simple, dichotomous, ternate or verticillate; fertile



1



2



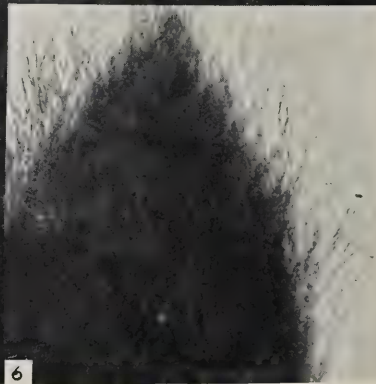
3



4



5



6

PLATE IV.

Types of Coremium in the Xylariaceae. I.

1. *Hypoxylon* (*Rosellinia*) *necatrix*: *Graphium* type, also known as *Dematophora*, on cotton plug. $\times 8$.
2. *Hypoxylon necatrix*: microscopic view of above. $\times 60$.
3. *Hypoxylon fragiforme*: coremia forming a circlet around the base of the developing stromata. This type has been called *Isaria umbrina* Pers. but it is closer to *Graphium*. $\times 8$.
4. *Hypoxylon oodes*: microscopic view of coremia structure similar to (3). $\times 60$.
5. *Hypoxylon cohaerens*: dendroid coremia, not arising in any particular order. $\times 8$.
6. *Xylaria digitata*: apex of fleshy coremium, *Isaria*-type. $\times 60$.

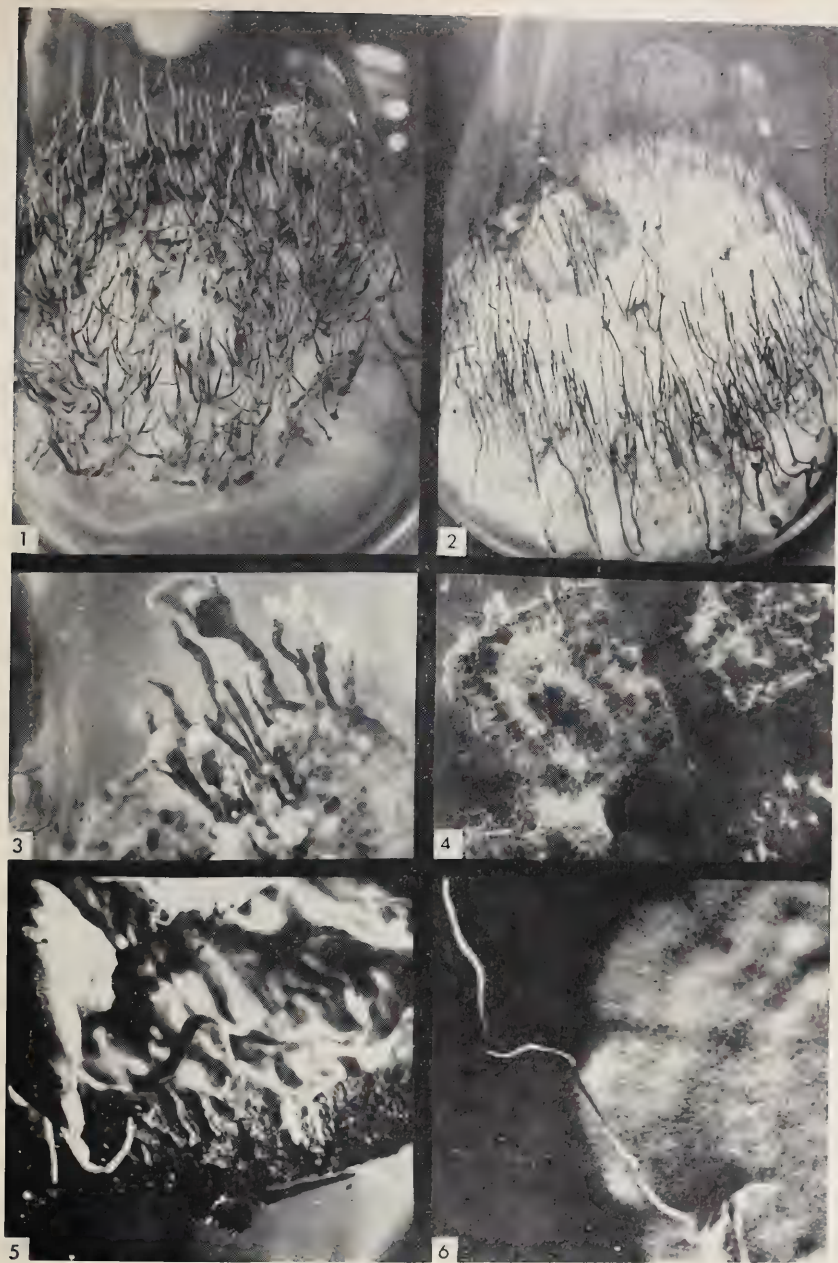


PLATE V.

Types of Coremium in the Xylariaceae. II.

1. *Xylaria subtrachelina*: general habit of coremia. } in flask culture, 14 days old on
2. *Podosordaria (Xylaria) sicula*: general habit of coremia. } 2% malt agar at 25°C. $\times 0.8$.
3. *Xylaria polymorpha*: general habit of spatulate and clavate coremia. $\times 0.8$.
4. *Xylaria fioriana*: acervular fruiting areas on agar surface. $\times 3$.
5. *Kretzschmaria heliscus*: variation from spatulate to aristate coremia. $\times 8$.
6. *Podosordaria pyramidata*: long dendroid covemium $\times 3$.

branches stout but not clavate, walls often smooth. This type is intermediate with *Sporothrix*, and is found in *Hypoxylon* section *Annulata* and in *Nummularia*.

- II. As above, but fertile branches clavate or swollen, usually with bulbous ends: (a) warted: *Hypoxylon* section *Applanata*

Daldinia (mainly) section *Euhypoxylon*

(b) not warted: *Xylaria*

Penzigia

- III. conidiophores themselves with characteristic long swollen clavate terminal regions off which a number, usually 50–100, of short clavate fertile branches arise. This is known as *Basidiobotrys* v. Hoehnel (1909), (Fig. V:6–10) and is structurally the most complex in the *Xylariaceae*. This stage has been described for *Hypoxylon punctulatum* by Barnett (1957), and is found in other species of the *Applanata* section of *Hypoxylon*.

In general we can conclude that there is a most interesting parallelism between conidiophore type and degree of stromal variation.

CONCLUSION

The problem of combining these characters discussed above so as to give the best possible classification is a formidable one. The objective approach to this will be the subject of a later paper. For the moment the author is content to decide the limits of the genera in the light of his own concepts. The many similarities between stromata that were formerly classed apart, and the correlation between perfect and cultural characters would seem to indicate that the twenty-one presently recognised genera contain many that are redundant, and that only twelve would appear to be valid.

There are also two persistent mistakes in nomenclature that must be corrected:

- (a) The genus *Anthostoma* Nitschke was made redundant by Traverso in 1906 and two genera *Anthostomella* and *Lopadostoma* substituted. Most of the species still wrongly ascribed to *Anthostoma* are clearly referable to *Anthostomella* as a succeeding paper will show.
- (b) The genus *Nummularia* Tulasne (1863) is invalid since it was preceded by *Nummularia* Riv. ex Rupp in 1745 and by its synonym *Numularia* Gilib. in 1781. Both these angiosperm genera are listed in *Index Kuensis*, edited by Hooker and Jackson (1895). House (1925) has correctly substituted the name *Numulariola*.

The main revisions in classification are summed up in the following key to the *Xylariaceae*:

1. Stromata small, one to few peritheciate, discoid or pulvinate or valsoid, erumpent or remaining immersed in the substrate; outer layer of substrate fused with the ectostroma and persistent around the rest of the stroma, sometimes blackened by it; basal tissue absent or slight; ostioles usually tubular, less commonly papillate or umbilicate
- 1' Stromata small to large, superficial or erumpent but not valsoid nor with substrate attached except around the margin, nor with tubular ostioles; basal tissue often slight but definitely present
2. Stromata valsoid, ascal plugs discoid or flattened
- 2' Stromata variable, discoid to pulvinate or aplanate effuse, ascal plug cubic or rectangular (Conidial stage: *Nodulisporium*)
- 3 (1) Stromata erumpent, perithecia immersed, basal tissue dark, carbonaceous layer well developed; stromata variable in form from aplanate to cylindric with no sharp demarcation; carbonous layer black or metallic with ectostroma sparsely retained or absent at maturity; perithecia usually close crowded, ovate or elongate; ascal plugs typically discoid or flattened. (Conidial stage: *Acrostaphylus* or *Basidiobotrys*)
- 3' Stromata superficial, or if erumpent then with well developed pale basal tissue or with perithecia clearly evident in outline
4. Stromata not extending far above substrate level, and if cylindrical not deeply cupulate; variable in shape or discoid or short cylindrical.
Numulariola sect. *Innata* Martin
syn. *Bolinia* Nits.
Camarops Karst.
Hypoxydon Bull sect. *Applanata* Mill.
Nummularia Tul.
Peridoxylon Shear.
Theissenia Maublanc.
- 4' Stromata conspicuously raised above substrate level, usually strictly cylindric and usually with cupulate apex.
Numulariola sect. *Camillea* (Fr.) Martin
syn. *Camillea* Fries.
5. Fertile part of the stroma large, robust, aplano-pulvinate to pulvinate or globose, multiperitheciate; perithecia immersed; interior either gelatinous and partly hollow, or corky and zonate with alternating light and dark zones, never concolorous
- 5' Fertile part of the stroma various in shape, but with a concolorous interior that is never gelatinous
6. Interior gelatinous, pale, with frequent cavities; ectostroma visibly coloured
- 6' Interior corky and zonate; if rarely partly gelatinous and hollow, then dark in colour; ectostroma pigmented though often dull at sight. (Conidial stage: *Sporothrix* or *Acrostaphylus*)
2. Lopadostoma (Nitschke) Trav.
3. *Anthostomella* Sacc.
- 4: *Numulariola* House emend. Martin.
5.
6.
7. *Entonaema* Möller
-
- Daldinia* C. & Dn.

- 7 (5) Stromata variable in shape but without well-defined ostioles, or ostioles sometimes tubular; entostroma with massive brittle carbonaceous outer layer; ectostroma heavily pigmented though dull at sight 8.
- 7' Not with this combination of characters 9.
8. Stromata simple or branched but not dendroid, sessile or stipitate; fertile clava globose or turbinate; ostioles obsolescent at maturity *Phylacia* Lev.
- 8' Stromata dendroid, usually multibranched, with perithecia borne latterly or in small terminal clavata; ostioles obsolescent or tubular *Thamnomycetes* Ehrenberg
- 9 (6) Stroma with no evident carbonaceous layer and pale inside; substrate usually non-lignaceous 10.
- 9' Stroma sometimes with no carbonaceous layer but then dark inside; carbonaceous layer accompanied by basal tissue of varying consistency and coloration from white to dark; substrate rarely non-lignaceous 11.
10. Ectostroma present, forming a white or brown covering; stromata often branched, with aplanate, discoid or urceolate clavulae. (Conidial stage: *Sporothrix* on *Isaria*-type coremium) *Poronia* Gleditsch
- 10' Ectostroma absent, stromata simple, fertile clavata pulvinate or aplanopulvinate. (Conidial stage: *Sporothrix* on *Isaria*-type coremium) *Podosordaria* E. & H.
- 11 (9) Perithecia predominantly vertical, if occasionally diagonal or lateral then basal tissue is corky and dark coloured; clavata sometimes club-shaped, more usually pulvinate, hemispheric or ovoid; stipitate or sessile; sterile apices excentric when present 13.
- 11' Perithecia predominantly lateral, if diagonally or vertically oriented then basal tissue is fleshy and white; fertile clavata or clavulae club-shaped or cylindric, stipitate or sessile; sterile apices centric when present. (Conidial stage: *Nodulisporium*, *Sporothrix* or *Acrostaphylus* on *Isaria*-type coremium) 12: *Xylaria* (including part of *Penzigia*) Hill ex Fr.
12. Stromata usually large, clavate, with bulbous apices and decussate or poorly differentiated stipes; stromal surface smooth; ectostroma continuous, typically bright-coloured; perithecia rarely evident in outline; subiculum infrequent. *Xylaria* section *Xyloglossa* Fries.
- 12' Stromata variable in size and shape but rarely bulbous, sometimes with sterile apices and usually stipitate; surface verrucose, rarely smooth; ectostroma usually fragmented, brown or black; perithecia usually evident; subiculum characteristic. *Xylaria* section *Xylorugosa* Martin
syn. *Xylaria* sections *Xylocoryne* Fries
Xylostyla Fries
Xylodactyla Fries.
- 13 (11) Perithecia not evident in outline though often few per stromal clava or clavula; if otherwise then the stromata terminate in definite excentric sterile apices; stromata are simple or branched, sessile or stipitate; clavata or clavulae pulvinate

- to obconic 14.
 13' Perithecia evident in outline, especially when
 few to a stroma, but never developing sterile
 apices 15.
 14. Stromata uniperitheciate or biperitheciate only.
Kretzschmaria Fr. sect. *Stilbohypoxyton*
 (Henn.) Martin.
 14' Stromata consistently with several perithecia,
 rarely uniperitheciate. (Conidial stage: *Acrostaphylus* on *Isaria*-type coremium).
Kretzschmaria Fr. sect. *Eukretzschmaria*
 Martin.
 15 (13) Stroma without evident colouration, nor producing
 a stain in acetone or alcohol; stromata with
 one, few or many perithecia, vertically oriented
 or occasionally diagonal but usually evident in
 outline; basal tissue discoloured or white but
 usually pale; ectostroma not coloured at matur-
 ity, continuous; ostioles papillate; ascal plugs
 cubic or rectangular. (Conidial stage: *Nodulisporium*,
 sometimes on a *Graphium*-type coremium).
Hypoxyton sect. *Entoleuca* (Syd.) Martin
 syn. *Hypoxyton* subsect.
Primocinerea Miller
 Part *Penzigia* Sacc.
 Part *Rosellinia* DN.
 15' Stroma brightly coloured or producing a stain in
 acetone or alcohol, if rarely failing this, then
 ostioles are umbilicate and the stroma is corky
 throughout; ascal plugs discoid or flattened.
 (*Graphium*-type coremium present sporadically) 16.
 16. Ostioles simple papillate. (Conidial stage:
Sporothrix).
Hypoxyton sect. *Papillata* Miller.
 16' Ostioles truncate papillate. (Conidial stage:
Acrostaphylus).
Hypoxyton sect. *Annulata* Miller.
 16'' Ostioles umbilicate, often wide and periphysate.
 (Conidial stage: *Sporothrix*, or *Acrostaphylus*).
Hypoxyton sect. *Euhypoxyton* Miller.

The rest of this work to be discussed in later papers amplifies the classification outlined here by reference to and discussion of the individual genera.

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